

NUMBERS OF BROODS PRODUCED BY THE CRAB SPIDER *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT. In coastal Maine the crab spider *Misumena vatia* produces a single brood of eggs, but incipient signs of double-broodedness occasionally appear: 1) hunting after guarding nest of first brood; 2) apparent laying of second brood by artificially provisioned individuals during an unusually warm summer; 3) and occasional production of second nests without eggs, accompanied by guarding. To determine whether these spiders are capable of producing a successful second brood, I provisioned adult females to enhance early laying of a first brood, removed them from their brood after 10 days, mated half of them a second time, and then provisioned them all again. Nearly two-thirds laid a second brood, whose success did not differ from that of unmanipulated *Misumena* first broods in the study area. Numbers of remated and non-remated females producing young did not differ, indicating that remating is not necessary for a successful second brood. However, five broods of non-remated spiders had low hatching success, suggesting that sperm were sometimes limiting. Semelparity in this population is thus apparently normally maintained indirectly by the length of the season.

Most temperate-zone spiders are reproductively active for a single year, probably a consequence of the adults' inability to survive the winter (Gertsch 1979). The reproductive effort itself may be divided into one or more broods, the number varying with the species and, at an intraspecific level, often with hunting success (Turnbull 1962; Kessler 1971; Schaefer 1976). Some species guard their broods (e.g., Fink 1986), thereby facilitating success, but lowering their opportunity for producing extra broods. Single-broodedness (semelparity) would be most likely expected among such species. In this context I define semelparity as the production of a single brood (one egg mass), as opposed to producing two or more broods at different times during a season (Fritz et al. 1982).

The crab spider *Misumena vatia* is generally considered to be semelparous (Gertsch 1939), and I have not observed it to produce more than one successful, natural brood at a northerly site along the Maine coast (Morse 1979, 1988). Since members of this population have a short reproductive season, and their egg masses average 65% of the maternal prelaying biomass (Fritz & Morse 1985), the question arises about what factors restrain these spiders from laying a second brood. Either the season might be too short for more than one brood (Fink 1986), or the brood might be too large to permit recovery for a second one (see Roff 1992; Stearns 1992). The cause-and-effect relationship between these two factors is

not clear in *Misumena*, nor is the degree to which its semelparity is genetically programmed.

Over this study (1977-present) I have obtained some suggestions that the semelparity observed is environmentally determined. 1) Some individuals resume hunting after leaving their broods and gain considerable biomass, which would be necessary to produce a second brood. 2) In 1991, an unusually warm summer, two individuals I had provisioned in the laboratory prior to egg-laying (first brood) in the field almost certainly produced second broods: nest building (Morse 1985) was followed by a striking loss of biomass like that accompanying egg-laying. The artificial provisioning permitted these spiders to complete their first brood earlier than they otherwise would have, facilitating the possibility of laying second broods generated from naturally-gained biomass. However, I was unable to verify that these putative broods produced young. One was preyed on, and the leaf on which the second nest was located fell off the plant and could not be found. 3) I have also occasionally found nests without eggs ("pseudonests") built by individuals that had already fledged a brood (12 out of 1434 egg-layers observed over nine years = 0.8%). This behavior demonstrates that previous egg-layers retain the behavioral traits associated with nest building, although it need not be associated with laying eggs.

Thus, the question of facultative iteroparity remained: even though it is highly likely that two

spiders laid a second set of eggs, I do not know whether the eggs were fertile. Although female spiders may retain sperm for considerable periods in viable form (Foelix 1982), it remains to be determined whether this holds for *Misumena*, or whether they retain adequate sperm for a second mating. These concerns may be important, because numbers of adult males decline rapidly between the first mating of females and when they complete caring for their brood (Morse, unpublished data).

An opportunity to test several aspects of this problem arose in the process of an unrelated experiment that required removal of broods from provisioned guarding female *Misumena*. I fed these individuals both before and after their first broods, so the results will not determine whether *Misumena* can successfully produce more than one brood in the study area, but they can answer several questions about whether iteroparity is possible or likely.

METHODS

Forty adult female *Misumena* were captured from milkweed (*Asclepias syriaca*) flowers during early July of 1993 and provisioned in the laboratory with large flies (Syrphidae, Sarcophagidae), moths (Noctuidae, Geometridae), and bumblebees (Apidae). These individuals had almost certainly not laid before. Individuals in the study area only rarely produce broods before 1 July (5 of 1615 broods from 1982–93: Morse, unpublished data), and those occasional individuals, easily identified by their extremely shrunk-abdomens, still guard their nests at this time. I also have no record of individuals that lay in one year surviving until the next (Morse, unpublished). After they commenced to refuse prey, the spiders were weighed and placed in screen cages (1.5 m \times 1.5 m \times 1.5 m, covered with standard metal window screening, open at the bottom) in the field that covered a single milkweed stem. Gravid females routinely place their egg-sacs in nests fashioned from the enclosed vegetation when placed in these cages (Morse 1985, 1990). All of the spiders laid on the milkweed after one to seven days. Screens were then removed, and parents were again weighed and then allowed to guard their broods until the broods were collected 10 days later.

At this time parents were again removed to the laboratory. As a result of losses from predation and handling, 36 adults were available for the experiment on semelparity. Within a day af-

ter collection, one-half of these spiders were mated with males that had been retained in the laboratory for unrelated breeding experiments. All the females were then provisioned further until they again began to refuse prey. They were then weighed and placed, as before, in screen cages, in the field to lay their eggs if they were inclined to do so. Those that laid a second brood were again weighed and then returned to their nests. At the end of the season all nests were collected for analysis. Offspring emerge from their nests in the second instar, leaving behind their first-instar cast skins, which provide an accurate record of success (Morse 1988).

Weighing spiders immediately before and after they lay permits calculation of the size of the egg mass, and in turn, the reproductive effort (biomass of eggs/biomass of female immediately before laying). Loss of biomass to production of silk and other factors at laying is 1% or less (Fritz & Morse 1985), and thus is not further treated in these analyses.

RESULTS

The experiment demonstrated unequivocally that the spiders can produce a viable second brood (Table 1), as 23 of the 36 individuals (63.9%) reared at least a few young in a second brood. Success of those that laid eggs (23 of 26: 88.5%) did not differ from that of unmanipulated spiders that laid eggs a first time in the same field (27 of 33: 81.8%) ($G = 0.51$, $P > 0.8$ in a G -test). It must be emphasized, however, that the second-nesters had in each instance already produced a successful first brood.

Remated individuals did not differ from non-remated ones in numbers of nests producing some young ($G = 1.09$, $P > 0.2$, G -test: Table 1), indicating that many of them retain viable sperm from earlier matings. A partial exception is that five broods of non-remated females had low success (7.8–37.4%, $\bar{x} = 21.0\%$ of the eggs hatched) (see Table 1), but none of those in which remating took place showed this pattern ($P = 0.031$ in a one-tailed Binomial Test). [For comparison, the four individuals with high but not complete success averaged 88.4% (79.8–96.9%) (Table 1)]. However, three remated individuals produced completely unsuccessful broods, for unknown reasons, although they all had apparently successful first broods (normal embryonic development took place). Additionally, a few individuals from both groups did not lay second broods, and a few from both groups died during provi-

Table 1.—Success of remated and not-remated spiders (*Misumena vatia*) in producing and rearing second broods to emergence from the nest.

Success	Remat- ed	Not remated
100% successful eggs	7	7
>50% successful eggs	3	1
<50% successful eggs	0	5
Eggs completely unsuccessful	3	0
Did not lay again	3	3
Died before laying again	2	2

sioning for a second brood (Table 1). Overall, similarities between the two groups greatly exceeded differences. The principal point of interest is that the majority of these provisioned individuals laid second broods, and most of their broods produced young.

Although body mass of the spiders averaged slightly larger after laying the first brood than after the second, this difference was not significant ($P > 0.05$ for both remated and unremated ones: one-tailed Wilcoxon matched-pairs, signed-ranks tests: Table 2). Assuming that the average difference between body mass following first and second broods represented the proportion of body mass not used for the first brood that was used for the second brood, over 95% of the resources used for the second brood must have been gathered between the two layings (Table 2).

No relationship occurred between the reproductive effort of the first brood and whether a spider laid a second brood ($P > 0.2$ in a one-tailed Mann-Whitney U Test). Spiders producing a second brood averaged a reproductive effort of $65.6 \pm 4.6\%$, $n = 26$, during their first brood; those that did not lay a second brood, the putative obligate semelparous individuals, averaged $66.7 \pm 4.7\%$, $n = 10$. Within the nonlaying group, reproductive effort did not differ between those dying before others laid a second brood ($66.2 \pm 2.7\%$, $n = 4$) and those surviving as long as those laying a second brood but not producing one themselves ($67.0 \pm 5.8\%$, $n = 6$).

DISCUSSION

Facultative semelparity.—Any change in fecundity, age at maturity, or age-specific mortality that reduces the value of adults and increases the value of juveniles will select for semelparity and against iteroparity (Young 1990; Stearns 1992). For instance, failure of an adult to acquire enough resources to breed in a particular year would force it to endure an additional winter, entailing high mortality and strong selection to shorten the life cycle. However, the investment by *Misumena* in a brood is extreme. Its extremely high reproductive effort, about two-thirds of body mass prior to egg-laying (Fritz & Morse 1985), exceeds that of coexisting hunting and sit-and-wait spiders [*Xysticus emertoni*, 45.0%; *Metaphidippus insignis*, 55.3%; *Phidippus clarus*, 63.5% (Morse, unpublished data)]. Further, a substantial percentage of guarding parents die before their young emerge from their nests slightly less than four weeks later (Morse 1987).

On the other hand, remaining resources permit survival for guarding a short time, and many individuals do live until their young emerge (Morse 1987). It may be that all the resources that can be exploited from the body at these times are used, and that the spiders' remaining resources merely happen to be adequate for them to survive. A perhaps revealing result relative to the argument about maximizing reproductive effort is that individuals laying two clutches under provisioned conditions registered a higher reproductive effort in the first brood than in the second, with over 95% of the resources for the second brood coming from new food captured after laying the first brood. Thus, the initial reproductive effort of these spiders appears to be as high as possible within their current morphological and ecological constraints; as noted, it exceeds that of coexisting spiders with comparable life styles. All of this information suggests that it would require a major evolutionary innovation in *Misumena* to increase its reproductive effort substantively. The machinery required for predation, plus the low metabolic rate of spi-

Table 2.—Biomass in mg, \pm SD, (mg) of spiders (*Misumena vatia*) following first and second clutches.

Treatment	<i>n</i>	First clutch	Second clutch	Second clutch as a proportion of first clutch
Remated	11	71.6 \pm 8.8	67.3 \pm 7.0	94.0%
Not remated	10	77.7 \pm 17.7	74.9 \pm 13.4	96.4%

ders (Foelix 1982), may account for the ability of most individuals to survive past this prodigious reproductive effort. Given these conditions, any opportunities that exist after the first brood are a bonus. There is no clear evidence that the spiders have compromised the first brood for the second; in fact, the relative reproductive efforts of the two broods counter the common prediction (Williams 1957) that reproductive effort will increase with brood, as reproductive value (potential volume of future reproductive output) decreases. The strength of the egg-laying response obtained in the experiment was therefore somewhat surprising.

The presence of the machinery for iteroparity where there has been almost continuous selection for semelparity raises an interesting question about the retention of variability in life history traits. Heritability of life history traits is on average lower than that of most other traits, although some variance usually remains (Mousseau & Roff 1987). The retention of variation in life history traits should depend on the age of the relationship, as well as the level of ongoing selection. If the trait exacted little cost, at some point selection toward obligate semelparity would be slowed, and vestiges of abilities for producing second broods might remain. Although semelparity is usually associated with big-bang reproduction, if organisms are often prevented from producing an extremely large brood (e. g., limited food supply: Fritz & Morse 1985), selection for an extreme condition should decline.

Predictions about neighboring populations.—The condition found and the behavior associated with it permit several predictions to be made about neighboring populations. To the south the longer season should permit a second brood, accompanied by reduced care of the first brood. It should favor such individuals to invest all remaining resources, limited as they may be, into guarding the second brood, although it would be interesting to determine whether guarding, shown in other contexts to be an extremely simply-triggered behavior (Morse 1989), will vary between broods. In populations to the north, one would not predict a striking change in behavior from that of my study area, since a spider should guard its brood as long as possible. However, the length of the guarding period may be curtailed, limiting its effectiveness, although the range of *Misumena* extends as far north along the eastern seaboard as Labrador (Dondale & Redner 1978).

The green lynx spider *Peucetia viridans* (Ox-

yopidae) exhibits increasing tendencies toward double-broodedness southward across central Florida (Fink 1986). However, its behavior, including hunting and constructing second egg sacs while still guarding, changes concurrently, and thus differs from any tendencies seen in guarding *Misumena*. Although guarding *Misumena* sometimes capture prey that visit their nest-sites, the sites at which they prefer to place their nests do not attract many prey, and this food never substantially increases their biomass (Morse 1987). The lynx spider's strategy would favor building nests at sites of active flowers. The favored nesting sites of *Misumena* are on milkweed, well after it has ceased to flower; further, they usually select nonflowering stems (Morse 1985). Goldenrods (*Solidago* spp.) are the principal field flowers in bloom during the height of the *Misumena* guarding period, and most of the local goldenrods have lanceolate leaves that would not provide satisfactory nesting sites. Thus, a foraging and nest-production shift similar to that of double-brooded lynx spiders would additionally require a simultaneous shift in nest-site selection (see Morse 1990).

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